Choloepus didactylus. By Peter J. Adam

Choloepus Illiger, 1811

Choloepus Illiger, 1811:108. Type species *Choloepus didactylus.*

CONTEXT AND CONTENT. Order Xenarthra (= Edentata), Suborder Pilosa, Infraorder Tardigrada, Family Megalonychidae, Genus *Choloepus,* which includes two species, *C. didactylus* and *C. hoffmanni* (distinguished below in Diagnosis section).

Choloepus didactylus (Linnaeus, 1758)
Linné's Two-toed Sloth

Bradypus didactylus Linnaeus, 1758:34. Type locality "Zeylona." Restricted to "Suriname" by Thomas, 1911:132.
Choloepus unau Link, 1795, in Cabrera, 1957:211.
Choloepus curi Link, 1795, in Cabrera, 1957:211.
Choloepus guianensis Fitzinger, 1871:399. Type locality "Guiana und Suriname."
Choloepus braziliensis Fitzinger, 1871:403. Type locality "Nord-Brasilien."
Choloepus didactylus var. *columbianus* Gray, 1871:432. Type locality "Columbia" [Colombia].
Choloepus florenciae Allen, 1913:469. Type locality "Florencia (alt. 1000 ft. [305 m]), Rio Bodoquera, Caquetá, Colombia."
Choloepus napensis Lönnberg, 1922:18. Type locality "along river Napo, altitude 2000 ft." [610 m], Napo province, Ecuador.

CONTEXT AND CONTENT. Familial designation of two-toed sloths (*Choloepus*) has been problematic, and they have historically been placed with three-toed sloths (*Bradypus*) in the Bradypodidae or alone in the Choloepidae. Most workers now agree that *Choloepus* belongs in the Megalonychidae, formerly a family with only extinct members (Engelmann, 1985). Consequently, traditional groupings of extinct "ground" sloths and extant "tree" sloths are no longer valid (Webb, 1985). No true subspecies of *C. didactylus* have been described but, if western and eastern populations gain subspecific status, three names are available (*C. d. columbianus, C. d. florenciae,* and *C. d. napensis*—Wetzel, 1982). The type specimen of the purported subspecies *C. d. pallescens* Lönnberg, 1928:12 (type locality "Perú, San Martín, Calavera") actually belongs to the species *C. hoffmanni* (Wetzel, 1982).

DIAGNOSIS. *Choloepus didactylus* (Fig. 1) can be distinguished from *C. hoffmanni* by having throat pelage that is similar in color to pectoral hair, whereas throat hairs are lighter in *C. hoffmanni.* In *C. hoffmanni,* cheek and throat hairs are distinctly shorter and finer than those of the neck and shoulder, but these hairs are not shorter in *C. didactylus.* The skull of *C. didactylus* (Fig. 2) is marked by an anterior maximal interpterygoid width that is at least double the minimum posterior interpterygoid width (less than double in *C. hoffmanni*), and by the presence of one pair each of small and large foramina penetrating the anterodorsal portion of the interpterygoid space (one pair of small and two pairs of large foramina in *C. hoffmanni*). Posterior foramina do not penetrate pterygoid sinuses in *C. didactylus,* but do in *C. hoffmanni.* In *C. didactylus* pterygoid sinuses are broadly inflated (greatest width >14 mm), but less so in *C. hoffmanni* (greatest width <13.5 mm). Maxillae of *C. didactylus* are in broad contact with the frontals, but are separated externally by lacrimals or nasals in *C. hoffmanni.* Cervical vertebrae usually number 7 (range 6–8) in *C. didactylus,* and 6 (range 5–6) in *C. hoffmanni* (Wetzel, 1985).

GENERAL CHARACTERS. Linné's two-toed sloth ranges from tan to buffy brown in color but in the wild may take on a slight greenish tinge due to green algae living on its hair (Aiello, 1985). Underfur is absent, and ventral pelage is usually lighter than that of the back. The long fur (up to 170 mm—Anderson and Jones, 1984) is parted along the ventral midline of the animal and is directed dorsally, collecting into a whorl at the level of the sacrum. Pinnae are reduced and completely concealed by hair. The light brown face is not furred and has a leathery texture. Young *C. didactylus* tend to have a darker pelage that is soft and woolly (Veselovsky, 1966).

The eyelids are fleshy and the eyes appear beady. Irises are reddish-brown and pupils are round (Meritt, 1985). A single pair of mammae is situated pectorally. Only a non-prehensile, vestigial tail remains. Manual and pedal formulae are 0-3-3-0-0 and 0-3-3-3-0, respectively. The digits of all four feet are syndactylous, and each bears a strongly curved claw. The naked volar surfaces of the feet are covered entirely with smooth, brownish-pink or brown pads. *C. didactylus* is nocturnal and spends much of its waking time hanging below branches in an inverted posture, often resting on a lower branch for support.

Mean measurements ($\pm SD$) for adult *C. didactylus* are as follows: total length, 677 ± 55 mm ($n = 41$); length of tail, 23 ± 7 mm ($n = 11$); length of hind foot, 148 ± 17 mm ($n = 37$); length of ear, 28 ± 4 mm ($n = 19$); mass, 6.07 ± 1.09 kg ($n = 21$); greatest length of skull, 111.2 ± 5.7 mm ($n = 42$); ratio of mini-

FIG. 1. Female *Choloepus didactylus* at the Calgary Zoo, Botanical Garden and Prehistoric Park in a typical suspensory pose. Photograph by D. H. Bininda.
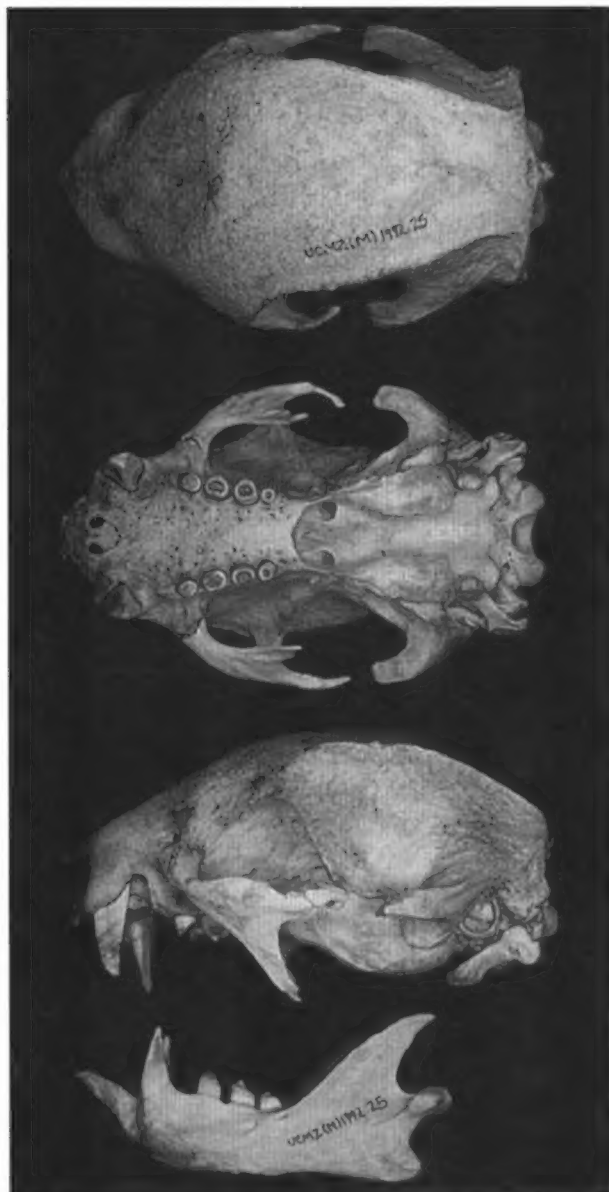
FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Choloepus didactylus* (sex unknown) from the Calgary Zoo, Botanical Garden and Prehistoric Park (University of Calgary Museum of Zoology UCMZ(M)1992.025). Greatest length of cranium is 11.8 cm. Photograph by H. I. Rosenberg.

mum to maximum interpterygoid widths, 0.47 ± 0.08 mm ($n = 30$—Wetzel, 1985). Sexual dimorphism is not marked (Anderson and Jones, 1984).

DISTRIBUTION. *Choloepus didactylus* is found in humid, warm, neotropical lowlands and is limited to well-established forest habitat to an altitude of 2,438 m (Britton, 1941). It is distributed (Fig. 3) as follows: north to the Río Orinoco delta in Venezuela and upper (Meta) Orinoco drainage in Colombia; east to Guyana, Surinam, French Guiana, and Maranhão state in Brazil; south along both banks of the Río Amazonas-Solimões; west to the Amazon basin of Colombia, Ecuador, and Peru (Wetzel, 1982, 1985). Deforestation may be reducing the natural range of *C. didactylus* (Wetzel and de Avila-Pires, 1980). *Choloepus* is known only from Recent times but may have originated in the Miocene (Patterson and Pascual, 1968).

FORM. With the exception of vibrissae and hair around the eyes (Britton, 1941), hairs of *Choloepus* are unique among mammals in having 8–11 longitudinal furrows extending along their length (Aiello, 1985; Wujek and Cocuzza, 1986). This fluting at-
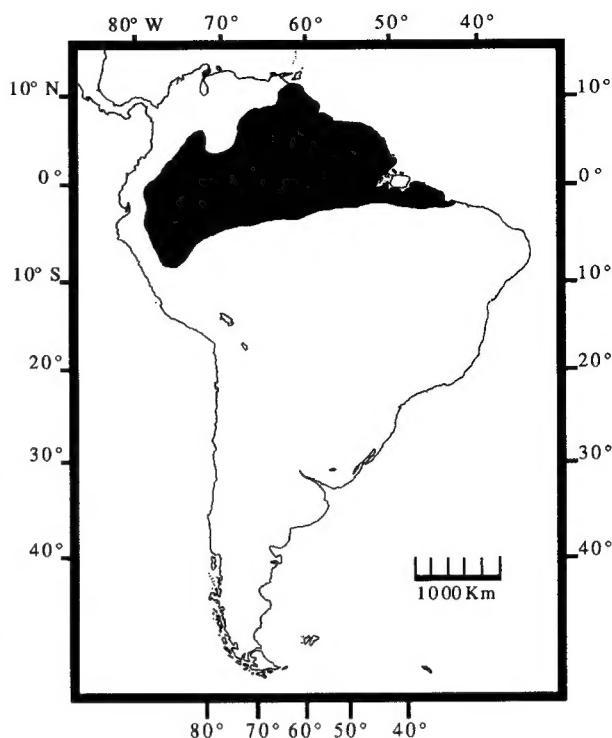

FIG. 3. Distribution of *Choloepus didactylus* in South America (modified with permission from Wetzel, 1982).

tenuates toward the distal end of each hair, and adjacent ridges are connected by cuticular bridges (Aiello, 1985). Hairs reportedly lack a central medulla and pigment granules (Aiello, 1985), although Wujek and Cocuzza (1986) dispute the absence of the medulla. Hair tracts along the body and limbs are directed dorsally. Skin of the body is 2–4 mm thick (Grassé, 1955), and that of the manus and pes confers syndactyly to the distalmost interphalangeal joints of the digits. The epidermal-dermal junction of the digital skin can be microscopically distinguished from other areas of the body by the presence of papillae. Dermatoglyphics, sweat glands, and calluses are lacking on the glabrous volar pads, but flexion creases are prominent. These pads are also one of the few places where fat deposits occur (Mendel, 1981*a*, 1981*b*, 1981*c*).

The skeleton of *C. didactylus* is illustrated in Grassé (1955: 1190). Vertebral number is variable, with ranges of 6–8 C, 23–25 T, 3–4 L, 4 S, and 4–6 Ca (total range 45–46—Frenchkop, 1953; Grassé, 1955; Wetzel, 1985). Transverse processes of posterior lumbar vertebrae may fuse with the ilium, and anterior caudal vertebrae often articulate tightly with the ischium. The resultant long and rigid pelvic girdle may provide stability previously provided by the extra vertebral processes (xenarthroses) that characterize the Order Xenarthra, but which have been secondarily lost in this species (Frenchkop, 1953). Both scapulae and clavicles are large in association with a strong forelimb (Frenchkop, 1953; Miller, 1935). Detailed distal skeletomuscular and joint anatomy of *Choloepus* limbs has been described (Mendel, 1979, 1981*b*, 1981*c*, 1985; Miller, 1935). Both manus and pes have marked flexibility in the mesopodia, but metapodial-phalangeal and interphalangeal joints are of the tongue-and-groove type. Only digits II and III of the manus remain functional; metacarpal V is absent, and I and IV are reduced to stubs. Metacarpal I consists of three centers of ossification: diaphysis, epiphysis, and a carpal element, the trapezium, fused to it (Flower, 1873). Pedal digits II, III, and IV are present, and metatarsals I and V are vestigial. Ungual phalanges each bear a strongly curved claw that is subequal in size to others of the same foot.

The skull of Linné's two-toed sloth is short and rounded dorsally. Adjacent bones are usually solidly fused in adults, making recognition of suture lines difficult. Strong temporal fossae are present, but a sagittal crest is lacking. The zygomatic arch is incomplete and has a pronounced, descending, jugal process. Tympanic bullae are absent. A prenasal bone is present (Grassé, 1955; Wetzel, 1985). The precise dental formula of *C. didactylus* is disputed; five

teeth are present in each maxilla, and four in each dentary. The anteriormost maxillary and mandibular teeth are triangular in cross section and larger than more posterior cylindrical teeth. The anterior teeth may be canines, as evidenced by their large size and separation from more posterior teeth by a diastema (Grassé, 1955), or they may be caniniform premolars (Eisenberg, 1989; Frenchkop, 1953). The caniniform teeth bear sharp, bevelled occlusal surfaces and are self-sharpening. The remaining posterior teeth have occlusal surfaces with complex wear facets due to differential wear of inner and outer dentine layers (Naples, 1982, 1995). Histological preparations of *C. didactylus* teeth show a thick cementum layer and no enamel. The orthodentine has numerous vascular canals externally, but the central dentine is amorphous and lacks canals (Ferigolo, 1985). Dentaries are solidly fused at the mandibular symphysis (Naples, 1982).

Whole-body musculature of *Choloepus* has been described (Humphrey, 1870; Mackintosh, 1875; Windle and Parsons, 1899), as have muscles of forelimb (Mendel, 1981b; Miller, 1935), hind limb (Mendel, 1981c), mastication (Naples, 1985b; Sicher, 1944), tongue (Naples, 1986), and face (Naples, 1985a). Skeletal musculature is uniformly composed of red muscle tissue (Britton, 1941). Both fore and hind limbs have undergone blending of muscle and changes in muscle action, including the rearrangement of the mm. tibialis anterior and extensor hallucis longus to the flexor compartment of the foot, which increase force of flexion (Mendel, 1981b, 1981c, 1985; Miller, 1935). Ligamentum femoralis is absent, giving the hind limb a large degree of free rotation (Mackintosh, 1875). Fibers of the masseter muscle of *Choloepus* lie in an almost horizontal plane, taking origin from the descending jugal process (Naples, 1982, 1985b). The presence of a grooved palate, large tongue, and mandibular adductor muscles may be functionally related to eating in an inverted posture (Naples, 1986).

Values for red blood cells of *C. didactylus* are similar to those of other mammals, with cell count of $4.2–4.8 \times 10^6/mm^3$, cell longevity 130–135 days, and hemocrit 49–53% (Marvin and Shook, 1963; Spector, 1956). Values are relatively high for blood hemoglobin (17.1–19.7 g/100 ml), urea nitrogen (25–28 mg%), and cholesterol (250–260 mg%), but they are comparatively low for glucose (58–62 mg%), chloride (94–102 mole equivalents/l), and bicarbonate (18–22 mole equivalents/l). Blood pH is >7.44; pCO_2 is <29.7; pO_2 is <74.9; and white blood cell numbers are $10–33 \times 10^3/mm^3$ (Bush and Gilroy, 1979). The heart beats 70–130 times per minute at rest (Britton, 1941) and 48–108 times per minutes under anesthesia (Bush and Gilroy, 1979). Systolic blood pressure ranges are 120–140 mm Hg (Britton, 1941), and diastolic ranges are 110–160 mm Hg (Goffart, 1971). The heart of *C. didactylus*, relative to body mass, weighs 4.9–5.9 g/kg and has large auricles with remnants of the fetal sinus venosus and associated valves (Ehrat, 1943). The vena cava is double to the level of the renal arteries and attenuates anteriorly. Blood returning to the heart from the iliac veins is largely transported by an intervertebral vein, which lies to the right of the spinal cord and runs through the neural foramina of the lumbar and thoracic vertebrae between the sacrum and the level of the heart. It drains into either the azygous or jugular vein (Barnett et al., 1958). Extensive retia mirabilia are present on the medial side of both the fore and hind limbs (Grassé, 1955). Lung volume of *Choloepus* is large (60 ml/kg, relative to body mass—Goffart, 1971). At rest, *C. didactylus* draws 10 breaths per minute (Bopp, 1954).

The brain of *C. didactylus* has been illustrated by Richter and Bartemeier (1926) and described by Elliot-Smith (1898). General brain form suggests that the senses of touch, taste, and smell are good, but that sight and hearing are poor. Levels of various polypeptides (e.g., substance P, neurotensin, and cholecystokinin) from the spinal cord of *C. didactylus* are similar to those of other mammals studied (Yaksh et al., 1988).

Eyes of *Choloepus* are directed forward with a divergent angle of 34° and set with an interoccular distance of 45–47 mm (Goffart, 1971). The retina of *C. didactylus* has a laterally located area centralis with 1,000 ganglion cells per mm²; the peripheral density surrounding the area centralis is 100 cells per mm². The area centralis forms a lengthened visual streak along the superior-inferior axis (Andrade-da-Costa et al., 1989). It is disputed whether a tapetum lucidum is present (Britton, 1941) or absent (Goffart, 1971). Olfactory bulbs, tracts, and piriform lobes are large (Goffart, 1971). Ackerknecht's organ is also present (Coebergh, 1930). The cochlea of *Choloepus* is typically mammalian (Ramprashad et al., 1985),

and *C. didactylus* hears in the range 0.3–25.3 kHz at 100 dB, with optimum hearing in the range 2–8 kHz at 45 dB (Suga, 1967). M. tensor tympani is present but not attached to the malleus. The small, concealed pinnae of Linné's two-toed sloth may be poor at collecting sound (Goffart, 1971). The vestibular structure of *Choloepus* is not appreciably different from that of other mammals (Ramprashad et al., 1984).

Choloepus is a foregut fermenter (Bauchop, 1978). The stomach of *C. didactylus* is large and three chambered, with well-developed rugae on the interior surface. The large fundus has a short, cone-shaped cecum extending from its posterior margin. The pyloris is poorly developed, having only thin, muscular walls (Klinckowström, 1895). No ceca are present on the intestine, and the transition from small to large intestine is gradual (Goffart, 1971). The rectum is pouch-like and may store up to 1 kg of fecal material (Grassé, 1955). Unlike *Bradypus*, *Choloepus* has a gall bladder; it is located on the central lobe of the trilobed liver (Britton, 1941). The liver may (Wislocki, 1928) or may not (Grassé, 1955) rotate 135° during embryogenesis.

Kidneys are small, oval, smooth, have a well developed hilum, and are positioned low in the abdominal cavity near the level of the sacrum (Britton, 1941). The urinary bladder is large and thick walled (Goffart, 1971). External genitalia are small, inconspicuous, and similar in form in males and females, making sex determination difficult without close examination (McCrane, 1966) or internal inspection. Males have a small penis, and, as testes are intra-abdominal, males have no scrotum. The expanded coxal bones and inflexible pelvic region may prevent thrusting movements during copulation (Frey, 1994). It is disputed whether a prostate gland or seminal vesicles are present in *C. didactylus* (Wislocki, 1928).

In females, the mesosalpinx creates an ovarial pouch that conceals the bilobed ovaries (Goffart, 1971). The vagina is double in its posterior third, with two external openings separated by a septum vaginae (Britton, 1941; Wislocki, 1928). The placenta of *C. didactylus* is deciduate, labyrinthine, endotheliochorial, nodular-discoidal in form, and attaches to the fundus of the unicornuate uterus. The 12-cm umbilical cord attaches marginally to the developing fetus, with free membranes constituting half of the fetal surface. The amnion is anodular and attached firmly to the chorion. Endothelial cells of maternal tissue are prominent, but not invaded by the trophoblast (Benirschke and Powell, 1985).

Thyroid glands are paired, connected by a thin isthmus, and are reported to be either of relatively small size with low activity (Marvin and Shook, 1963) or actively secreting glands falling within the size range of most eutherian mammals (Goffart, 1971). Islets of Langerhans are present in the pancreas, and adrenal glands are located far anterior to the kidneys (Britton, 1941).

FUNCTION. The dorsal projection of hair tracts in sloths is thought to increase the efficiency of sloughing off of water while the animal hangs in an inverted posture (Goffart, 1971). Although generally lacking subdermal adipose tissue, the thick skin of *C. hoffmanni*, and presumably that of *C. didactylus*, is more insulative than that of most other tropical mammals (Scholander et al., 1950). The distensible fat tissue underlying hand and foot pads may act as a friction generator, conferring a firm grip and thus improving the ability of a sloth to hang onto overhead supports (Mendel, 1981b, 1981c).

Adaptations for suspensory locomotion are most prevalent in the skeletomuscular anatomy. Claws and syndactylous digits enable the manus and pes to function as hooks for moving below branches, and enhanced flexor musculature ensures that the grip is firm (Mendel, 1985). The anatomy of the limbs even allows dead sloths to hang from a support (Merrett, 1983). The broad thoracic cavity, with the support of many pairs of ribs, acts as a basket to support the viscera of the animal (Frenchkop, 1953).

The relatively high blood pressure of *C. didactylus* is needed to supply blood to the limbs, which lie above the heart in the usual posture of the animal (Goffart, 1971). Functions suggested for the retia mirabilia include blood storage or a means of preventing blood stoppage during prolonged muscle contraction (Goffart, 1971). In *C. hoffmanni* this vascular arrangement serves in thermoregulation as a countercurrent heat-exchanger (Scholander and Krog, 1957).

Decerebration lesions either above or below the red nucleus of the brain induce flexor rigidity, although the response is stronger and longer when a lesion is made above the red nucleus (Richter and Bartemeier, 1926). In most terrestrial mammals decerebration

causes extensor rigidity, presumably a response to increase the security of a normal tetrapodal stance. Flexor rigidity suggests that the nervous system is adapted to the hanging posture of *C. didactylus*. Decerebrate *C. didactylus* responded to the distress call of a young sloth (Richter and Bartemeier, 1926).

Vision in *Choloepus* is marked by poor accommodation, poor acuity, and slow light reactions of the iris (Mendel et al., 1985). Reactions to falling are likewise slow, and *Choloepus* that are falling distances of 4 m show no attempt to right themselves, even though falls of <3 m are known to break their spines (Goffart, 1971). The superior-inferior visual streak of the retina may increase acuity and depth perception of vertical objects in the visual field, such as a branch under which the animal is progressing (Andrade-da-Costa et al., 1989).

Food may be retained in the stomach of *Choloepus* for 70–90 hours post-ingestion and may take one week to pass through the entire gut (Britton, 1941). The large urinary bladder and rectal pouch allow considerable waste to be stored prior to elimination. Volumes of urine and solid waste expelled at any given time may be 500 and 235 ml, respectively, accounting for up to 30% of the total body mass of the sloth (Meritt, 1973). Urine retention may promote water resorption by cells in the wall of the urinary bladder (Goffart, 1971).

Blood-urea levels are high (100 mg/l—Britton 1941), and this nitrogenous compound may be used by gut bacteria for protein synthesis. The amount of uric acid in the urine is also high, but two-toed sloths are considered ureotelic (Goffart, 1971). The heart appears to be well supplied with glycogen (0.5–0.6 mg%). Both the adrenal glands and pancreas are important in carbohydrate management. Glycotaxis is apparently slow, as animals which have had their pancreas removed are hyperglycemic after only 3–4 days and die after one week (Britton, 1941).

ONTOGENY AND REPRODUCTION. No fixed breeding period is discernable for *C. didactylus*, as births and the carrying of young have been documented throughout all seasons of the year (Moeller, 1990). Mating occurs abdomen to abdomen and takes place either on the ground (Britton, 1941) or while hanging from a branch (Eisenberg and Maliniak, 1985; Veselovsky, 1966). Retention of wastes in the urinary bladder and rectum by *Choloepus* makes detection of pregnancy by palpation equivocal (Meritt, 1985). Determination of the gestation period in *C. didactylus* is difficult, and both sperm storage and delayed implantation are implicated in the wide range of estimates found in the literature (Van Doorn, 1971). The most reliable findings indicate that gestation lasts 10.5 months (Eisenberg and Maliniak, 1985; Partridge, 1991). Estrus in *C. hoffmanni* lasts 4–5 days and is marked by swelling of the labia, blood on perches, and presence of a scablike development in the vaginal opening (Meritt, 1985). A similar condition is likely for *C. didactylus*. Intercycle periods have not been reported.

The embryology of *C. didactylus* has not been documented. Young are born singly and head-first, with a mean mass at birth of 364 g and total length of ca. 250 mm (*n* = 3—Veselovsky, 1966). Newborns have open eyes and are partially precocial, being able to climb onto the mother's abdomen using a strong grip with little or no assistance (McCrane, 1966). Parturition in one instance took 35 minutes (Veselovsky, 1966). Post-parturition consumption of the placenta by the mother or other sloths is common (Britton, 1941; Van Doorn, 1971).

Suckling bouts are periodic, last 5–15 minutes, and take place opposite to the force of gravity, with the young situated on the ventrum of the hanging mother. Weaning is gradual and occurs ca. 2.5 months after birth. Solid foods are first taken at 3–5 weeks of age (Eisenberg and Maliniak, 1985; McCrane, 1966; Stone, 1957). A 1-week-old *C. didactylus* can drink water (Eisenberg and Maliniak, 1985). Young achieve independence gradually, beginning as early as 5 months of age when they weigh 15% of the mother's mass (Eisenberg and Maliniak, 1985; Stone, 1957). Mortality of infants in captivity is high. Of 21 births at the Prague zoo, 3 were stillborn and 13 died within the first 2 months of life (McCrane, 1966).

Early growth of *C. didactylus* has been documented (Eisenberg and Maliniak, 1985; McCrane, 1966; Veselovsky, 1966). Ca. 2.5 years are required for young to achieve adult body proportions (Veselovsky, 1966), but sexual maturity is not reached until the age of 3 years in females and 4.5 years in males. The oldest female

known to give birth was 25 years old (Eisenberg and Maliniak, 1985).

ECOLOGY. The natural habitat of *C. didactylus* is classified as an ever-wet tropical climate, with an annual rainfall of >2,000 mm and short dry-seasons (Sarmiento and Monasterio, 1975). Captive sloths prefer warm, humid conditions and may be kept at 21–30°C and 30% relative humidity in autumn and winter, and 20–38°C and 25–90% relative humidity in spring and summer (Eisenberg and Maliniak, 1985; Partridge, 1991).

Both genera of sloths, *Choloepus* and *Bradypus*, live in habitats with moderate or dense tree growth and prefer areas rich in labyrinthous lianas (vines). They often use these lianas and interconnecting tree crowns to move between adjacent trees (Montgomery and Sunquist, 1975, 1978). Although vines also extend from the canopy to the forest floor, *Choloepus* is typically found in the upper forest canopy at heights 24–30 m above the ground (Mendel, 1981*a*, 1981*b*). Most lianas and vines are <10 mm in diameter, although they may get as large as 100 mm. *C. hoffmanni* is most accomplished on supports <39 mm in diameter and reticent to traverse supports ≥65 mm in diameter (Mendel, 1981*a*). Similarities in limb size and anatomy may confer comparable limitations to *C. didactylus* (Mendel, 1981*b*, 1981*c*).

The nocturnal habits and camouflaged nature of sloths make examination of their diet difficult. *Cecropia* leaves are often stated to be the plant most consumed by sloths (e.g. Britton, 1941; Lundy, 1952), although this statement is more applicable to *Bradypus* (Meritt, 1976) and indirect evidence indicates that the diet of *Choloepus* may be considerably more varied. Although the diet of wild *C. didactylus* is not known, *C. hoffmanni* is found in association with at least 52 plant species, most of which are likely to comprise some part of the diet in the form of young shoots, leaves, and fruits (Montgomery and Sunquist, 1975, 1978). In captivity, *C. didactylus* eats a variety of foods, including salad, grain, leaves, cooked rice, carrots, kale, sweet potato, apples, and other fruits and vegetables (Eisenberg and Maliniak, 1985; Veselovsky, 1966). Cooked meat is also taken readily (Britton, 1941; McCrane, 1966), and wild sloths may opportunistically eat animal matter in the form of insects, eggs, nestlings, carrion, and small vertebrates (Meritt, 1985; Merrett, 1983). Coprophagy has been observed in captive animals (Partridge, 1991).

Data from an extensive rescue operation after flooding in Surinam indicate a density of 56 *C. didactylus* per km² (of an area of 15 km²). This equates to a biomass of 241 kg/km², or 7.9% of the total biomass of non-volant mammals rescued. Corresponding values for *Bradypus* from the same area were, density, 140/km²; biomass, 449 kg/km²; and total biomass, 14.7%. From these data, the energy intake of wild Linné's two-toed sloths was estimated at 220 kcal ha⁻¹ day⁻¹. However, these findings are probably not representative of their whole range (Eisenberg and Thorington, 1973).

Two-toed and three-toed sloths overlap considerably in occupancy of tree species (and individual trees), suggesting that they may compete for food and territory (Montgomery and Sunquist, 1975, 1978). *C. didactylus* shares most of its range with *Bradypus variegatus* and is also sympatric with *B. tridactylus* in Guyana, Surinam, French Guyana, and northern Brazil; and with *C. hoffmanni* in Peru (Wetzel, 1982). Many tree species are also used by phyllophagus monkeys, and competition for food may occur (Montgomery and Sunquist, 1975). Below-branch feeding, as exhibited by *Choloepus* (Naples, 1986), may reduce competition with above-branch foragers (Grand, 1972). Regardless, the impact of sloths on vegetation may be less than that of monkeys because sloths have a lower metabolic demand and more specialized gut (Montgomery and Sunquist, 1975). In captivity, Linné's two-toed sloths are kept successfully in habitats with marmosets (*Callathrix jacchus*), pacarana (*Dinomys branicki*), tamarins (*Saguinus labiatus*), agoutis (*Dasyprocta aguti*), hairy armadillos (*Euphractus villosus*), and nine-banded armadillos (*Dasypus novemcinctus*—Merrett, 1983).

Principal terrestrial and arboreal predators of *Choloepus* are the coati (*Nasua nasua*), jaguar (*Panthera onca*), marguay (*Felis wiedii*), ocelot (*F. pardalis*), and anaconda (*Eunectes murinus*—Britton, 1941; Goffart, 1971; Moeller, 1990). The threat to sloths from these predators is greatest when sloths descend to the ground to defecate or change trees (Moeller, 1990). The harpy eagle (*Harpia harpyja*) is the major airborne predator of sloths (Izor, 1985; Retting, 1978). Many native South American cultures consider the

killing of sloths to be taboo (Britton, 1941), and hunting of *C. didactylus* is not extensive.

Sloths are unusual in having an extreme diversity of arthropod associates, although two-toed sloths lack an underfur and tend to have fewer ectoparasites than do three-toed sloths (e.g., 50% of the tick load of *Bradypus*—Waage and Best, 1985). Hematophagous insect parasites of *C. didactylus* include *Clerada apicicornis* (Hemiptera: Lygaeidae), biting flies (Culicidae, Psychodidae, Tabanidae), and some triatomine bugs. The mallophagan louse *Lymeon gastroides* has been found on hair of *Choloepus didactylus*. Two tick specialists on sloths are *Ambyomma geayi* and *A. varium* (Ixodidae). Sloth mites (Psoroptidae) tend to aggregate near or inside the anus and may be coprophagous or predatory. The mite *Edentalges choloepi* is known from *C. didactylus* (Waage and Best, 1985). Non-ectoparasitic arthropods carried by *C. didactylus* include chrysaugine pyralid moths (e.g., *Cryptoses choloepi*). Although sloth moths may inhabit the hair of sloths during all stages of life, the larvae of at least some of these insects live in sloth dung and presumably establish a phoretic relationship with sloths as adults (Waage and Best, 1985; Waage and Montgomery, 1976). Eye and nasal feeding by moths was observed by Lundy (1952), but Waage and Montgomery (1976) believe that these insects usually feed on sebaceous secretions or rainwater trapped in the fur. The distribution and density of sloth moths may vary seasonally and geographically (Waage and Best, 1985).

The grooved and wettable hairs of *Choloepus didactylus* promote algal growth that gives the animal a greenish tinge in the wild and helps to camouflage it among the greenery of its habitat. The symbiotic algae of two-toed sloths include *Cyanoderma choloepi* and *Trichophylus*. *Choloepus didactylus* may also benefit from these algae in the procurement of nitrogen either by licking or by diffusion of nitrogen through the hair to the skin (Aiello, 1985). Wild animals do not generally possess algal growths until the 2nd month of life (Goffart, 1971).

Hemoflagellate parasites of *C. didactylus* include *Endotrypanum schaudinni*, *Leishmaniau braziliensis*, and *Trypanosoma mesnilbrimonti* (Dedet et al., 1989; Shaw, 1985). Nematode fauna of two-toed sloths includes *Bostrichodera bequaerti*, *Dioctophyme renale*, and *Diptetalonema spiralis* (Frimeth and Arai, 1984; Goffart, 1971). The bacteria in the gut of sloths have not been identified (Bauchop, 1978). *C. didactylus* hosts Jari, yellow fever, and Anhanga viruses (Seymour, 1985; Seymour et al., 1983). Encephalitis, a mosquito-born virus, also occurs in *C. didactylus* (Waage and Best, 1985).

The oldest captive *C. didactylus* on record was 27 years of age (Moeller, 1990); longevity is usually estimated to be 30–40 years (Merrett, 1983; Moeller, 1990). Most dead two- and three-toed sloths in the wild are found during the rainy season, as colder temperatures may affect their ability to digest food (Montgomery and Sunquist, 1978).

Low and high frequency transmitters are useful for locating sloths in their complex three-dimensional habitat (Montgomery and Sunquist, 1973). Although often thought to be slow and docile, *Choloepus* have efficient clawing and biting abilities (Montgomery and Sunquist, 1978; Partridge, 1991). A combination of tiletamine HCl and zolazepam (Parke, Davis & Co., Ann Arbor, MI) at a dosage, relative to body mass, of 1.9–6.0 mg/kg is sufficient for anesthetizing *C. didactylus* (Bush and Gilroy, 1979).

BEHAVIOR. The behavior of *C. didactylus* is poorly documented, due to their nocturnal habits with peak activity during crepuscular hours (Conway et al., 1977; Howarth and Toole, 1973; Partridge, 1991), and due to the great heights and complex habitat in which they live (Mendel, 1981a). Most zoos use a reversed night/day cycle in sloth enclosures to enable patrons to observe these animals during their short bouts of activity. An activity budget for captive animals follows: sleeping, 45% of the time; resting with eyes closed, 20%; awake but inactive, 10%; and active, 25% (Bopp, 1953, 1954).

Wild *Choloepus* are typically found alone unless a mother is with her young (Goffart, 1971), but captive specimens may be kept successfully in small groups. Two mother *C. didactylus* with young avoided direct contact with each other in captivity (Van Doorn, 1971). Fighting between two males (one of which died as a result) presumably vying for access to a female has been observed (Partridge, 1991). Pre-mating courtship has not been reported for *C. didactylus* (Merrett, 1983), but a female *C. hoffmanni* in estrus

may approach and rub her anogenital region against a male. Males typically respond by going to sleep (Meritt, 1985).

In captivity, other individuals may approach a mother during parturition and aid in the process by preventing the newborn from falling. They also clean the mother and young (McCrane, 1966). Mutual grooming is uncommon except when a mother cleans her young of feces and urine (Veselovsky, 1966). Captive-born *C. didactylus* begin to self-groom at 4 weeks of age, and exhibit sniffing, licking, tasting, and fighting play behaviors in the 5th week of life (McCrane, 1966). Mothers are very protective of their young if they are in contact (Lundy, 1952), and when a mother and her young are separated, the latter may give a distress call in the form of short bleats 1.4 kHz in frequency (Ramprashad et al., 1985). Young that fall to the ground call frequently, but may die after unsuccessful attempts by the mother to find them. As adults, *C. didactylus* are only able to hiss (Goffart, 1971). Young are known to become distressed by bright light (McCrane, 1966).

When not active, *C. didactylus* generally assumes one of two positions. In the first, the sloth rests its back or sacral region on top of the base of a branch and hangs onto an overhead support with one, two, or three limbs (Bopp, 1954). Partridge (1991) reports that a vertical separation of 30–40 cm between branches is most comfortable for *C. didactylus* resting in this position. The second posture is known as the hanging basket; in this case, support is maintained by both hind limbs while the head and forelimbs are curled ventrally over the groin (Bopp, 1954).

Locomotion in two-toed sloths has been well documented (Anthony, 1907; Mendel, 1979, 1981a, 1981b, 1981c, 1985; Schneider, 1940). When moving in trees, *C. didactylus* suspends itself below branches by all four limbs. This posture may give these animals better access to leaves and branches (Britton, 1941), reduce joint strain, and dampen body oscillations and early swing-phase potential energy during movement. The under-branch posture also tends to minimize problems of balance (Mendel, 1979, 1985). Limb-swing phases occur in contralateral, diagonal couplets when moving under supports (Anthony, 1907; Mendel, 1981a; Schneider, 1940). Average and maximum speeds of 0.5–0.6 km/h and 1.6 km/h, respectively, have been reported for captive *C. didactylus* traversing below supports (Merrett, 1983; Schneider, 1940), but no data are available for wild animals. No leaping occurs, and changes of direction on branches are made by supporting the entire weight of the body with the hind limbs while twisting and stretching the anterior half of the body (Mendel, 1979, 1981c). *C. didactylus* is an agile swimmer (Britton, 1941; Lundy, 1952).

Choloepus didactylus descends from the forest canopy only to defecate or change trees. Movement on the ground is slow (0.25 km/h), awkward, and may expose sloths to terrestrial predators (Anthony, 1907; Miller, 1935; Preble, 1924). Descent occurs head first, unlike the backward descent of *Bradypus* (Mendel, 1981a). During typical terrestrial locomotion, weight is carried on the elbow and ulna of the forelimb and ankle or volar surface of the hind limb (with the pes rotated 45° laterally). Elbows, hips, and knees remain flexed in all phases of the walk. Limbs are swung uncoupled for short (10–30 cm), distances, thus a stable, tripodal stance is maintained at all times (Anthony, 1907; Schneider, 1940).

Defecation and urination occur simultaneously near the base of a tree at 3.4–4.6 day intervals (Eisenberg and Maliniak, 1985). Unlike *Bradypus*, two-toed sloths do not bury their waste, which is recognizable as exposed piles of small dense pellets 8–12 mm in diameter (Waage and Best, 1985). In captivity, groups of *C. didactylus* tend to defecate simultaneously, indicating social or metabolic facilitation (Eisenberg and Maliniak, 1985). Infants descend to the ground and evacuate independent of their mother at 22 weeks of age (McCrane, 1966).

Cropping of food in *Choloepus* is accomplished by protrusion of the mandible and biting of vegetation with the caniniform teeth. Mastication is open-mouthed and unilateral, with lateromedial movement of the jaw at a rate of 0.55–0.59 s per cycle (Naples, 1985b; Sicher, 1944). Both fore and hind limbs are employed to pull branches toward the mouth (Preble, 1924), and relatively large chunks are chewed and swallowed (Naples, 1985b). *C. hoffmanni* eats 340 g of wet food and 170 ml of water per day, and similar amounts are likely to be taken by *C. didactylus* (Meritt, 1985). Food intake by captive *C. didactylus* drops slightly before defecation (Meritt, 1973). Water is taken by lapping at a rate of 0.45 s per lap (Bopp, 1954).

Licking, scratching, and rubbing of the body on branches are

common grooming behaviors. *Choloepus* may scent mark territories in a manner similar to *Bradypus* (Goffart, 1971). Scratching occurs in occasional bouts lasting several minutes and employs both fore and hind limbs, although only the fore limbs are used to scratch the face (Bopp, 1954). Wetting of the fur by two-toed sloths has been observed in temperatures >30°C, and panting and sweating are believed to be ineffective in cooling of these animals. Under heat stress, captive *Choloepus* display increased fighting and actively seek shade. When cold, they do not shiver. Muscles may enter hypertonus or the animal may curl into a hanging basket posture to conserve heat (Goffart, 1971).

Choloepus occurs more often in zoos and adjusts better to captivity than does *Bradypus*, which does not eat in captivity. *Choloepus* is notorious for its greater tendency to fight when handled (Meritt, 1982; Partridge, 1991). The caniniform teeth may be used in both display and physical defense (Naples, 1985b).

GENETICS. *Choloepus* is unusual in that it has at least seven distinct karyotypes, consisting of a variable, and often odd, number of unpaired and highly polymorphic chromosomes. The diploid number of *C. didactylus* may range from 52 to 64 and includes 3–15 submetacentric, 11–23 acrocentric, 2–4 metacentric, and 2–7 unpaired chromosomes. Supernumerary chromosomes are classified according to size and shape; euchromatism indicates that these elements are genetically active (Jorge et al., 1985).

Sex-determining mechanisms for *C. didactylus* are unclear. Sonta et al. (1980) suggest that in their male specimen, autosome 21 became translocated onto the Y chromosome resulting in an unpaired chromosome 21. They propose that the sex determining mechanism is thus a variation of the XO-XY type. Jorge et al. (1985) believe that females are represented by XX or XO sex chromosome pairs, and that males have atypically large and polymorphic Y chromosomes. The study by Jorge et al. (1977) indicates that hybrid offspring may result from a mating between a male *C. didactylus* (identified as *C. hoffmanni florenciae* by Jorge et al., 1977) and a female *C. hoffmanni*.

REMARKS. *Choloepus didactylus* is also known as the unau. The generic name is derived from the Greek *kholos*, meaning lame, and *pous*, meaning foot. The Greek words *di-*, meaning twice, and *daktulos*, meaning finger or toe, make up the specific epithet. Both terms refer to the reduced digital formula of the manus.

The biologies of *C. didactylus* and *C. hoffmanni* are often considered to be very similar. However, few data are available to validate this assumption. In general, more is known about Hoffmann's sloth due to extensive research on Barro Colorado Island in the Panama Canal (Montgomery and Sunquist, 1973, 1975, 1978). For more information not presented here on two-toed sloth biology at the generic level, Goffart (1971) should be consulted for an excellent review and extensive citation list.

Two interesting aspects of sloth physiology remain unstudied in *C. didactylus*. The first is imperfect homeothermy, as the only published record of body temperature in Linné's two-toed sloth is by Bush and Gilroy (1979), who found that body temperature was always <34.4°C. *C. hoffmanni* exhibits a wide range of body temperatures, with rectal temperature ranging from 33.4 to 36.2°C within a 24-hour span (Goffart, 1971).

Sloths are also well known for their 'slothfulness.' Another unstudied aspect is basal metabolic rate, which has not been measured for *C. didactylus*. It is estimated that oxygen consumption would be 0.188 cm^3 g^{-1} h^{-1} for *C. hoffmanni* (45% of that expected from body mass), with no rise even during pregnancy (McNab, 1978, 1985, 1987). A number of hypotheses have been advanced to explain this low metabolism, including low-caloric and high-fiber diet, possible presence of toxins in the diet, relatively low muscle mass, low blood pressure, and low glycogen reserves (Goffart, 1971; McNab, 1978). Two-toed sloths also have slow muscles (although faster than *Bradypus*), and isometric twitches in *C. hoffmanni* skeletal muscle may be one-sixth as fast as those of a cat, with recovery times being 9–14 times longer. This muscle slowness is poorly understood, as fine structure of their muscle fibers resemble the typical mammalian arrangement. Low ATPase activity and differences in sarcoplasmic reticulum and mitochondrial distributions have been implicated (Bárány et al., 1967; Goffart, 1971).

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